



COMPARATIVE MORPHOLOGY OF THE SALDIDAE AND MESOVELIIDAE (HETEROPTERA)*

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I. INTRODUCTION

There has been little agreement among heteropterists on the probable position of the Saldidae in the higher classification of the Heteroptera, and this family, more than any other, has been variously moved from one group to another. Recently, on the basis of his studies of the female genitalia of the Heteroptera, SCUDDER (1959) suggested that the Saldidae might be closely related to the Mesovelidiidae. A comparative morphological study of these two families was, therefore, thought to be necessary to throw some light on the probable position of the Saldidae, and its relationship with the Mesovelidiidae. Both alate and apterous forms of the two families have been studied and their morphology is compared and discussed.

In addition, two general aspects of the morphology of the Heteroptera have been considered namely, the interpretation of the head sclerites and the variation in the thoracic structure between apterous and macropterous forms of the two families.

II. MATERIALS AND METHODS

Saldula palustris (Douglas) was collected from the beach at Point Grey, Vancouver, B.C. *Aepophilus bonnairei* Sign. from Jersey, Channel Islands, was kindly supplied by Dr. G. G. E. SCUDDER of the University of British Columbia. *Mesovelia mulsanti* White from England and Holland were obtained from Mr. I. LANSBURY (Hope Department of Entomology, Oxford) and Dr. R. H. COBBEN

*) Based in part on a thesis submitted in partial fulfilment of the requirements for the degree of Master of Science of the University of British Columbia, Vancouver, B.C.

(Wageningen, Netherlands), respectively. The alate specimens of *Mesovelia vittigera* Puton were obtained from the Musée Royal de L'Afrique Centrale, Tervuren, Belgium, and were originally collected in the Congo. Other specimens of the families belonging to the four higher taxonomic groups — Pentatomomorpha, Cimicomorpha, Amphibicorisae and Hydrocorisae — were also used for comparative study.

The external anatomy was studied both from dried and alcohol-preserved specimens. The material was boiled in 10% potassium hydroxide, passed through glacial acetic acid, stained in acid fuchsin, and cleared in creosote. Observations on the cephalic muscles of *Saldula* were made from specimens preserved in 70% alcohol, passed through different grades of alcohol, cleared in xylene and examined under polarized light.

All drawings were made by using a squared graticule eye piece, and are not made to the same scale.

III. COMPARATIVE DESCRIPTIONS

Head*)

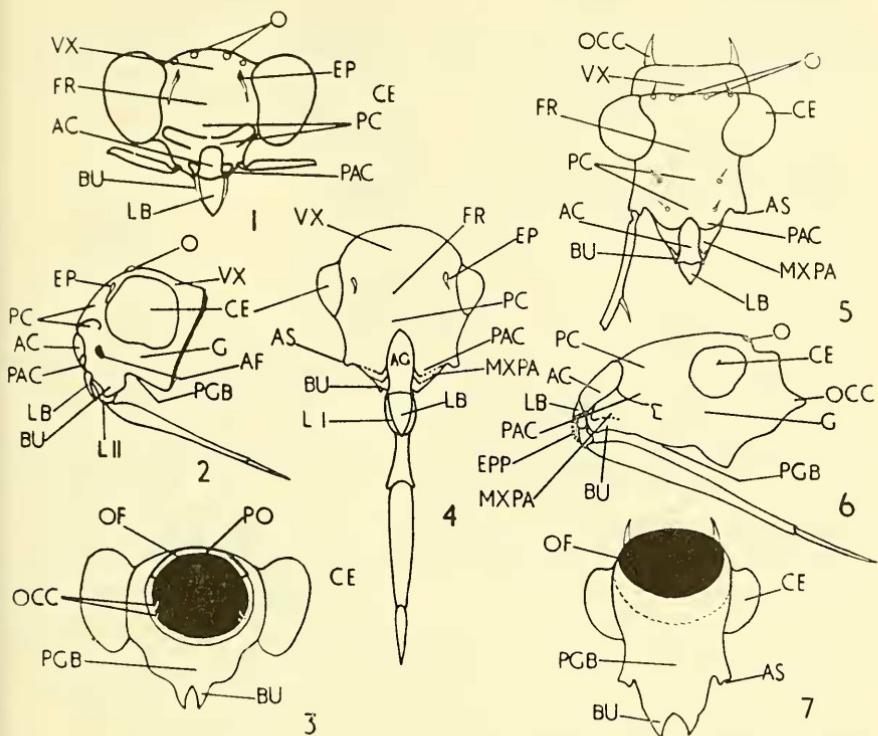
Saldula palustris (Douglas) (Figs. 1—3)

Head short, broad, vertex well developed, with a lateral invagination near eye extending anteriorly to frons; coronal and ecdysial cleavage lines distinct in nymph, absent in adult; frons short, frontoclypeal sulcus absent; clypeal region relatively extensive, differentiated into postclypeus, anteclypeus and paraclypeus, cephalic portion of postclypeus with two lateral unpigmented areas; bucculae well developed; postgenal bridge short; mandibular plate absent, mandibular lever well developed, triangular (in nymph and adult); postocciput in the form of thin ring around occipital foramen, apparently differentiated into dorsal and lateral elements, lateral parts bearing paired condyles; labrum broad and flap-like, reaching distal end of second labial segment, epipharyngeal process absent; labium four-jointed, first segment thickest, third longest, being swollen proximally and tapering distally; antennae four-segmented with small intersegmental sclerites, first segment much thicker than rest, the whole beset with hairs, third and fourth segments also bearing stout bristles; eight to ten pairs of trichobothria present, scattered over vertex, frons, and postclypeus (nymph with four pairs, one pair on frons, two pairs on postclypeus and fourth pair on anteclypeus); compound eyes conspicuous, two ocelli present; two unpigmented areas present laterad of ocelli.

Aepophilus bonnairei Sign. (Fig. 4)

Similar to *Saldula* in essential parts, but differing in following features. Cephalic portion of postclypeus without two lateral unpigmented areas, paraclypeal region not as well defined as in *Saldula*, restricted to upper two thirds of anteclypeus; maxillary plate area well developed; bucculae not well developed; labrum

*) The terminology of parts follows that of SNODGRASS (1960).



Figs. 1—3. Head of *Saldula*. (1) dorsal (frontal) view; (2) lateral view; (3) ventral view. Fig. 4. Head of *Aepophilus bonnairei*, dorsal view. Figs. 5—7. Head of *Mesovelia mulsanti*: (5) dorsal view; (6) lateral view; (7) ventral view

reaching distal end of first labial segment, and not second as in *Saldula*; compound eyes not conspicuous, ocelli absent; postocciput not divided into dorsal and lateral elements; postgenal bridge longer than in *Saldula*; four pairs of trichobothria — one pair on frons, two pairs on postclypeus and one pair on anteclypeus.

Mesovelia mulsanti White (Figs. 5—7)

Head longer than in *Saldula*; vertex well developed, and overlapped by prothorax; coronal and frontal ecdysial cleavage lines indistinct in nymph and adult; frontoclypeal sulcus absent; clypeal region well developed, differentiated into postclypeus, anteclypeus and paraclypeus; maxillary plate area well developed, separated from paraclypeal region by a short genal sulcus; lower limit of maxillary plate area delimited by an indistinct line; bucculae poorly developed; mandibular plate absent, mandibular lever well developed, roughly quadrangular; labrum flap-like, with an epipharyngeal process extending almost to distal end of second labial segment; postgenal bridge longer than in *Saldula*; postocciput indistinguishable from occiput, and bearing two dorso-lateral condyles; labrum four-jointed; first segment thickest, third longest, being swollen on inner side proximally and tapering distally; antennae four-jointed with small intersegmental sclerites, first antennal

segment thicker than rest, bearing a stout bristle lateromedially; three pairs of trichobothria, one pair on frons, two pairs on postclypeus (in the nymph one additional pair on anteclypeus); compound eyes inconspicuous, ocelli rudimentary.

Mesovelia vittigera Puton

Similar to *M. mulsanti* but ocelli well developed.

Thorax

Saldula palustris (Douglas) (Figs. 8—13, 30—34)

Prothorax. Pronotum large, with anterior collar, posteriorly overlapping base of fore wings, callal area broad, dome-shaped and triangularly depressed in middle; episternum shorter than epimeron, forming a precoxal shelf, pleural sulcus and pleurodema distinct but short; trochantin short, very distinct in nymph; sternum differentiated into a transversely elongated presternum, a triangular basisternum, and a sternellum, furcal arms elongate, extending laterally to meet pleurodema.

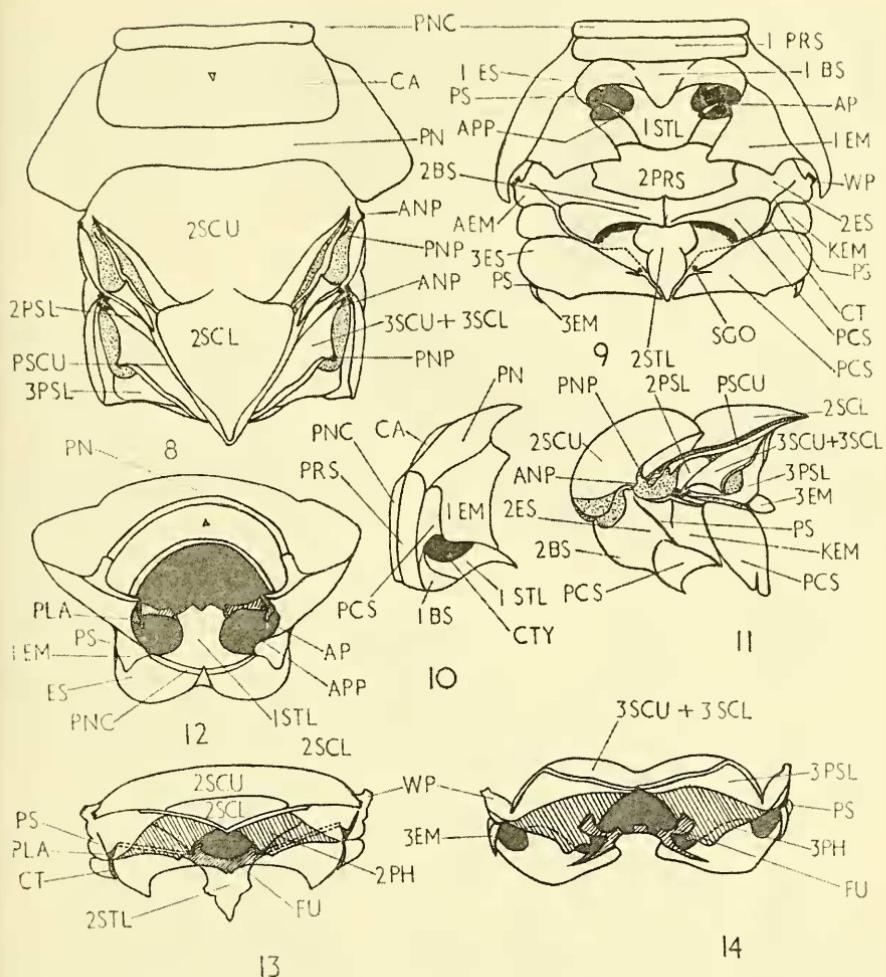
Mesothorax. Mesonotum differentiated into scutum and scutellum, with dividing sulcus incomplete, scutum secondarily divided into a median and two lateral areas, scutellum extending posteriorly over second abdominal segment, and apically pointed, parascutellum extending anterolaterally into scutoscutellar region, the latter being unequally sclerotized, postscutellum visible laterally; pleural sulcus distinct, short, pleurodema short, directed anteriorly; trochantin short; episternum forming precoxal shelves, epimeron divided into a dorsal anepimeron and a ventral katepimeron, the latter produced into a point at lower limit of coxal cleft; pleural wing process very distinct; basalar and subalar sclerites not distinguishable; sternum well developed, and divided into a presternum, a basisternum, and a sternellum, the latter extending posteriorly over metasternum; furca well developed, with furcal arms extending laterally and meeting pleurodema; phragma well developed.

Metathorax. Metanotum in the form of fused metascutum and scutellum, postscutellum well defined; pleural sulcus horizontal, and dorsal in position, pleurodema short; trochantin comparatively long; episternum broad, forming a large precoxal shelf, two precoxal shelves being approximated medially, epimeron small and dorsal in position; orifice of scent-apparatus located laterally; basalar and subalar sclerites indistinguishable; metapleural wing process lying forward in region of mesepimeron, and reinforced by processes from postscutellum and epimeron of mesothorax and postscutellum of metathorax; metasternum reduced to a small plate beneath mesoscutellum; furcal arms short, not reaching pleurodema; phragma very large.

Wings (Figs. 30, 31)

Fore wings differentiated into clavus, corium, embolium, and a membranous area, posterior end of clavus produced medially into a narrow triangular area along inner margin of membrane, membranous area with four cells.

Hind wings with distinct vannal and jugal folds, costa, subcosta and base of



Figs. 8—14. Thorax of *Saldula*: (8) dorsal view; (9) ventral view; (10) lateral view of prothorax; (11) lateral view of pterothorax; (12) internal view of prothorax showing pleurodema and apodemes; (13) internal view of mesothorax showing furca, phragmata and pleurodema; (14) internal view of metathorax showing furca, phragmata and pleurodema

radius fused, radius and media distally fused, base of media and cubitus in contact with distal median plate, two vannal veins in the vannal area, 2V with a thickened base, jugal lobe with single jugal vein; humeral plate well developed, first and second axillaries reduced, third axillary articulated both with proximal median plate and second axillary, two median plates (proximal and distal) present.

Legs (Figs. 32—34)

Coxae, especially those of hind leg, well developed, having only pleural and trochantinal articulations, hind coxa with inflected articular surface, proximal half

with a coxal suture, internal ridge of suture continuous with inflection of articular surface, fore and middle coxae without coxal suture, distally coxae bearing anterior and posterior articular surfaces for articulation with trochanter, trochanter immovably articulated with base of femur; femora flattened laterally; hind tibia longer than hind femora, bearing stout bristles, proximal end with a distinct head bent toward femur; tarsi consisting of three tarsomeres, the basal the smallest, tarsomeres with bristles, pretarsus in the form of two claws.

Aepophilus bonnairei Sign. (Figs. 15—17)

Prothorax. Pronotum large with a pronotal collar; epimeron broader than episternum, precoxal shelf formed by both; pleural sulcus and pleurodema short; coxal cleft prominent, trochantin present; sternum differentiated into a basisternum and sternellum; furcal arms short.

Mesothorax. Mesonotum a triangular piece; pleural sulcus short (shorter than that of prothorax); trochantin present; sternum differentiated into a presternum, basisternum and sternellum, latter extending over metasternum (as in *Saldula*); furca not well developed.

Metathorax. Metanotum undifferentiated, shorter than pronotum and mesonotum; pleural sulcus dorsal in position; epimeron dorsal; pleurodema very short; episternum broad, forming a large precoxal shelf.

Legs. Coxae more or less like those of *Saldula*, no outer suture and inflection, anterior and posterior articular processes present, femora flattened laterally, hind tibiae longer than hind femora as in *Saldula*, tibiae with stout bristles at their distal ends, tarsi with three tarsomeres.

Two rudimentary mesothoracic wings present.

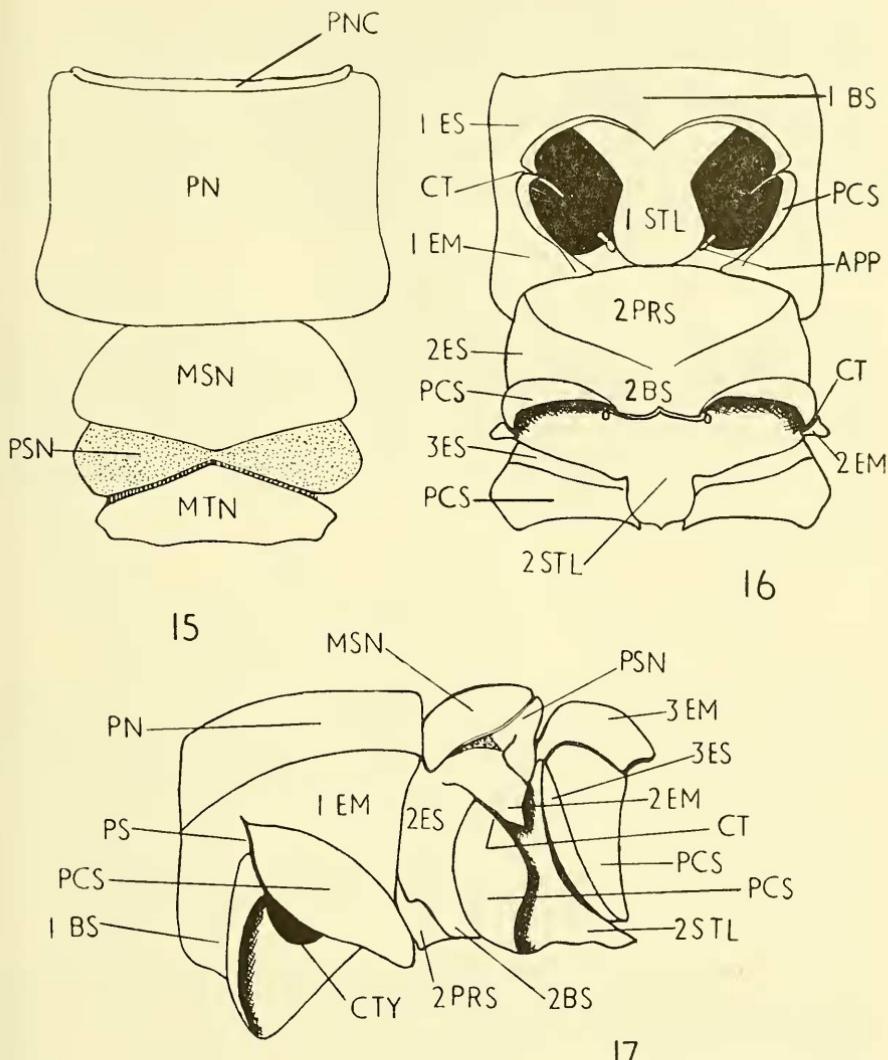
Mesovelia mulsanti White (Figs. 18—23)

Prothorax. Pronotum large, with a short collar; epimeron broader than episternum, precoxal shelf formed by both episternum and epimeron; pleural sulcus indistinguishable, a very short pleurodema present; trochantin present, very distinct in nymph; sternum differentiated into a basisternum and a sternellum; furcal arms (apophyseal apodemes) small, pointing ventro-posteriorly.

Mesothorax. Mesonotum undifferentiated; pleural sulcus indistinguishable, very short pleurodema present; episternum medially fused with basisternum; trochantin present; precoxal shelf formed by both episternum and epimeron; sternum differentiated into basisternum and sternellum; furcal arms (apophyseal apodemes) short, pointing posteriorly.

Metathorax. Metanotum undifferentiated; pleural sulcus indistinguishable; coxal cleft absent (present in prothorax and mesothorax); apophyseal apodemes short, pointing laterally; episternum fused with basisternum, forming a part of precoxal shelf; metasternum differentiated into basisternum and sternellum, latter fused with first abdominal sternite; single median orifice of scent apparatus present.

Legs. Coxae well developed, fore and middle coxae being swollen, articulation both pleural and trochantinal, hind coxae without coxal sutures on their outer



Figs. 15—17. Thorax of *Aepophilus bonnairei*: (15) dorsal view; (16) ventral view; (17) lateral view

surfaces; trochanter immovably attached to base of femur, femora flattened laterally, fore and middle femora with more stout bristles than hind femora, hind tibiae with stout bristles, middle tibiae with combs at their distal ends, three tarsomeres, pretarsus in the form of claws, latter provided with pseudoaroliae (parempodium).

Mesovelia vittigera Puton (Figs. 24—29)

Prothorax. Pronotum with anterior collar, posteriorly overlapping bases of fore and hind wings, pronotum with a wide callal area, the latter with two laterally

located depressions; epimeron broader than episternum; pleural sulcus short, pleurodema very short; trochantin present; sternum as in *M. mulsanti*.

Mesothorax. Mesonotum differentiated into scutum and scutellum, the latter not extending posteriorly over second abdominal segment as in *Saldula*; postscutellum present; sternopleural region the same as in *M. mulsanti*.

Metathorax. Metascutum and scutellum fused, median part extending over second abdominal segment; postscutellum distinguishable; pleurosternal region the same as in *M. mulsanti*.

Wings (Figs. 28, 29)

Fore wings with clavus, corium, an indistinct embolium, bases of costa, subcosta, radius fused, distal ends of fused costa, subcosta and radius, and media and cubitus form a stigma, rest of wing membranous, but without cells.

Hind wings without jugal fold, vannal fold present, bases of costa, subcosta, radius and media fused, radius and media distally fused, two vannal veins present.

Legs. As in *M. mulsanti*.

Abdomen

Saldula palustris (Douglas) (Figs. 35—39, 45, 46, 50)

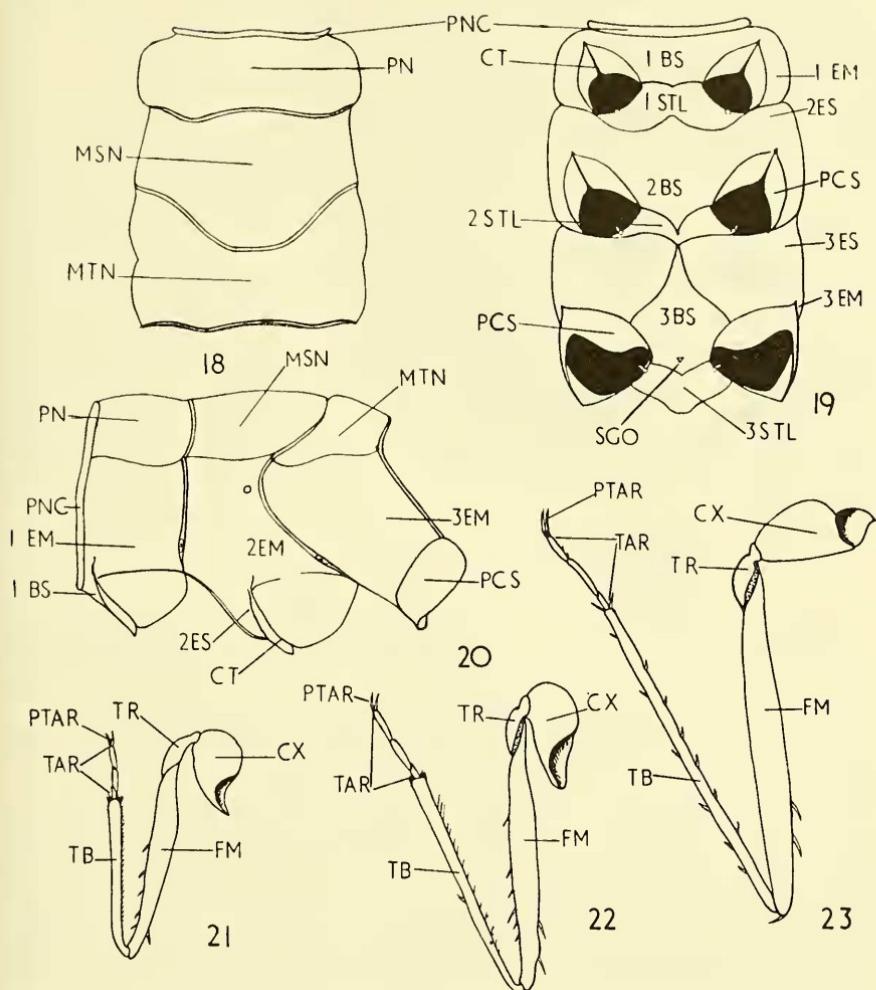
Abdomen with ten segments. Terga of segments two to eight differentiated into dorsal median plates and lateral paratergites, tergum of first segment not complete medially, in the male posterior margin of second paratergite modified into a granulated convex lobe; conjunctiva between second and third paratergite forming beneath the anterior margin of third paratergite a fold with a concave anterior margin, the latter being beset with stout setae; this together with convex lobe of second paratergite forms, during copulation, grasping mechanism in male; remnants of orifices of abdominal scent-glands present at posterior margin of third tergite.

Sternum of first segment rudimentary and indistinguishably fused with partially membranous sternum of second segment; seven pairs of spiracles present on lateral margins of sterna two to eight.

Female genitalia (Figs. 36—39)

Previous descriptions: EKBLOM (1926); LESTON (1956); SCUDDER (1959).

First gonapophyses joined by membrane, elongate, tapering and split longitudinally with serrate dorsal tips, rami sclerotized; first gonocoxa fused with ventral part of eighth paratergite; ninth tergum without separate paratergite; gonangulum triangular, its anterior limbs being fused with first ramus, and posterior side with ninth tergum, ventral angle of posterior side articulating in a notch on middorsal side of second gonocoxa, thus forming a fulcrum on which the latter pivots; second gonapophyses broader than first, sclerotized and united except at apices, the latter being truncate; second gonocoxa elongate and thickened dorsally; gono-



Figs. 18—20. Thorax of *Mesovelia mulsanti*: (18) dorsal view; (19) ventral view; (20) lateral view. Figs. 21—23. Legs of *Mesovelia mulsanti*: (21) fore leg; (22) middle leg; (23) hind leg

places broad, curved and free distally, united proximally by partially sclerotized membrane; spermatheca single, with an oval bulb or receptacle, and an elongated spermathecal tube; the latter communicating with vagina, a muscular pump with a single flange present between receptacle and main part of duct; wall of vagina lined internally with wrinkled chitinous intima, and strengthened by a sclerotized ring.

Male genitalia (Figs. 45, 46, 50)

Previous descriptions: EKBLOM (1926); MARKS (1951); PRUTHI (1925). Aedeagus differentiated into phallosoma and endosoma, the latter being further

divisible into conjunctiva and vesica; proximal part of phallosoma wide and membranous, distal part being narrow, heavily sclerotized and bent over proximal part, mouth of phallosoma located ventro-laterally and confined to its distal half, two minute posteriorly-directed appendages located one on each side of the anterior end of mouth, base of phallosoma supported by an inverted Y-shaped sclerite, with its upper limb fused with junction of basal plates; dorsal half of conjunctiva sclerotized, forming a curved sclerite with its two ends produced into lateral "wings" on either side of mid-dorsal line, distal end of conjunctiva containing two pairs of dorsolaterally located appendages, anterior pair smaller than posterior one, ventral wall of conjunctiva containing near mouth of phallosoma a V-shaped structure with two pairs of processes projecting anteriorly from inner angle of V, inner pair being smaller than outer; vesica narrow, coiled, and in close contact with ejaculatory duct; ejaculatory reservoir located at junction of conjunctiva and vesica; basal plates completely fused in middle line, forming horseshoe-shaped structure; capitate processes attached on to ends of basal plates; parameres long, sickle-shaped, and pointed at apices, proximal ends being broader and curved for muscle attachment.

Aepophilus bonnairei Sign. (Fig. 47)

Abdomen with ten segments. Terga two to eight differentiated into median tergites and lateral paratergites; first tergum fused with second; clasping organ present in second and third segments.

First sternum rudimentary and indistinguishably fused with partially membranous second sternum; seven pairs of spiracles on segments two to eight.

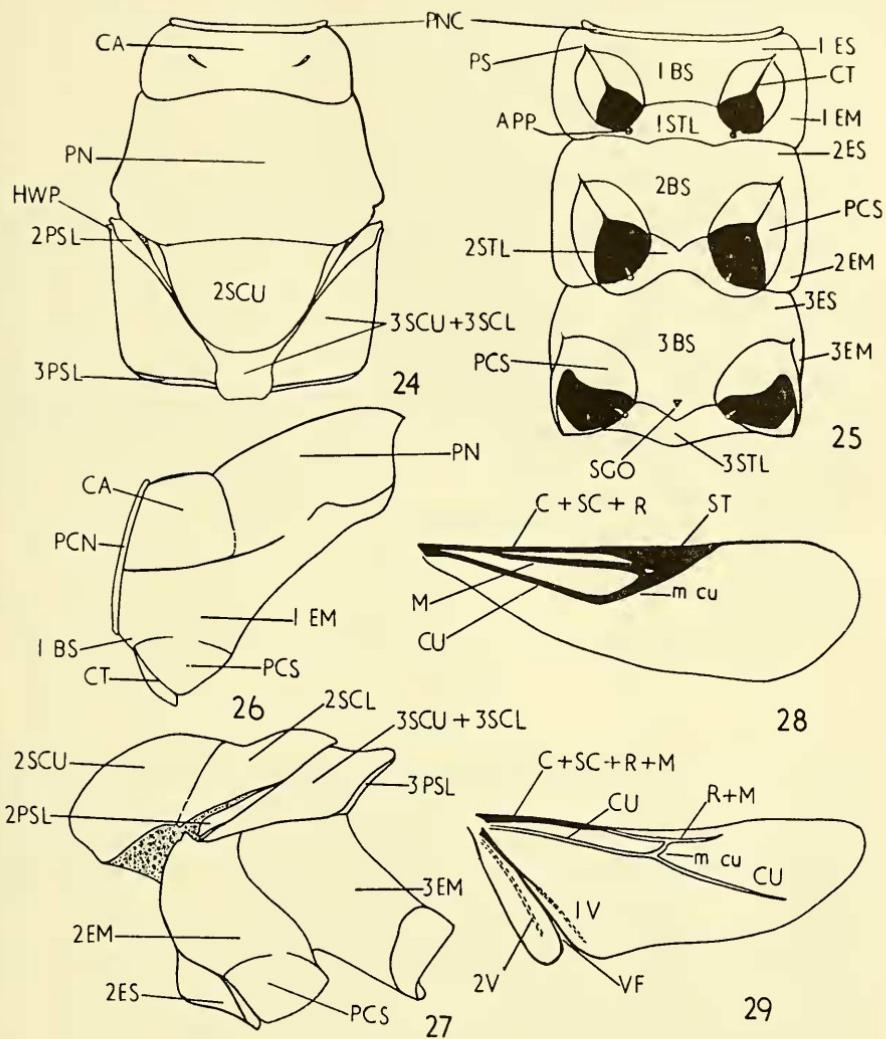
Female genitalia. More or less as in *Saldula palustris*.

Male genitalia (Fig. 47). Aedeagus differentiated into a phallosoma and endosoma, the latter with two appendages projecting out of mouth of phallosoma, base of phallosoma membranous, distal part narrow and heavily sclerotized, bent over proximal part, base of phallosoma supported by an L-shaped sclerotized structure, horizontal limb being fused with junction of basal plates; dorsal part of endosoma presents a sclerotized structure; basal plates completely fused and like those in *Saldula*.

Mesovelia mulsanti White (Figs. 40—44, 48, 49, 51)

Abdomen with ten segments. Terga of segments two to eight in female and two to seven in male differentiated into dorsal median tergites and lateral paratergites; orifice of abdominal scent-gland in middle of fourth tergum; clasping organ in male absent.

First sternum indistinguishably fused anteriorly with metasternellum and posteriorly with second sternum; seven pairs of spiracles present on segments two to eight; anterior margin of seventh sternum produced anterolaterally in mid-line as a long apodeme; two circular patches of black setae present on eighth sternum in male.



Figs. 24—27. Thorax of *Mesovelia vittigera*: (24) dorsal view; (25) ventral view; (26) lateral view of prothorax; (27) lateral view of pterothorax. Figs. 28—29. Wings of *Mesovelia vittigera*: (28) fore wing; (29) hind wing

Female genitalia (Figs. 41—44)

Previous description: EKBLOM (1926); NEERING (1954); PENDERGRAST (1957); SCUDDER (1959).

First gonapophyses joined by membrane, elongate, tapering and split longitudinally, with serrate tips; rami sclerotized and interlocking; first gonocoxa fused with eighth paratergite; gonangulum triangular, its posterior side also fused with an inflection between eighth and ninth terga; second gonapophyses elongate, scl-

rotized, laciniate, united except at tips; second gonocoxa elongate; gonoplacs triangular, sclerotized, curved and attached to second gonocoxae; spermatheca single with an accessory fecundation canal.

Male genitalia (Figs. 48, 49, 51)

Previous description: EKBLOM (1926); PRUTHI (1925).

Aedeagus differentiated into phallosoma and endosoma, the latter being further divisible into conjunctiva and vesica; proximal part of phallosoma membranous, distal part heavily sclerotized and bent over proximal part; a triangular sclerotized area present in mid-dorsal part of conjunctiva, proximally conjunctiva produced into sclerotized appendages projecting from mouth of phallosoma; vesica narrow and short, in close contact with ejaculatory duct; two ejaculatory reservoirs distinguishable; basal plates completely fused in middle line, forming a horseshoe-shaped structure; capitate processes attached laterally; parameres hook-like, pointed at apices, proximal ends being broader for muscle attachment.

Mesovelia vittigera Puton

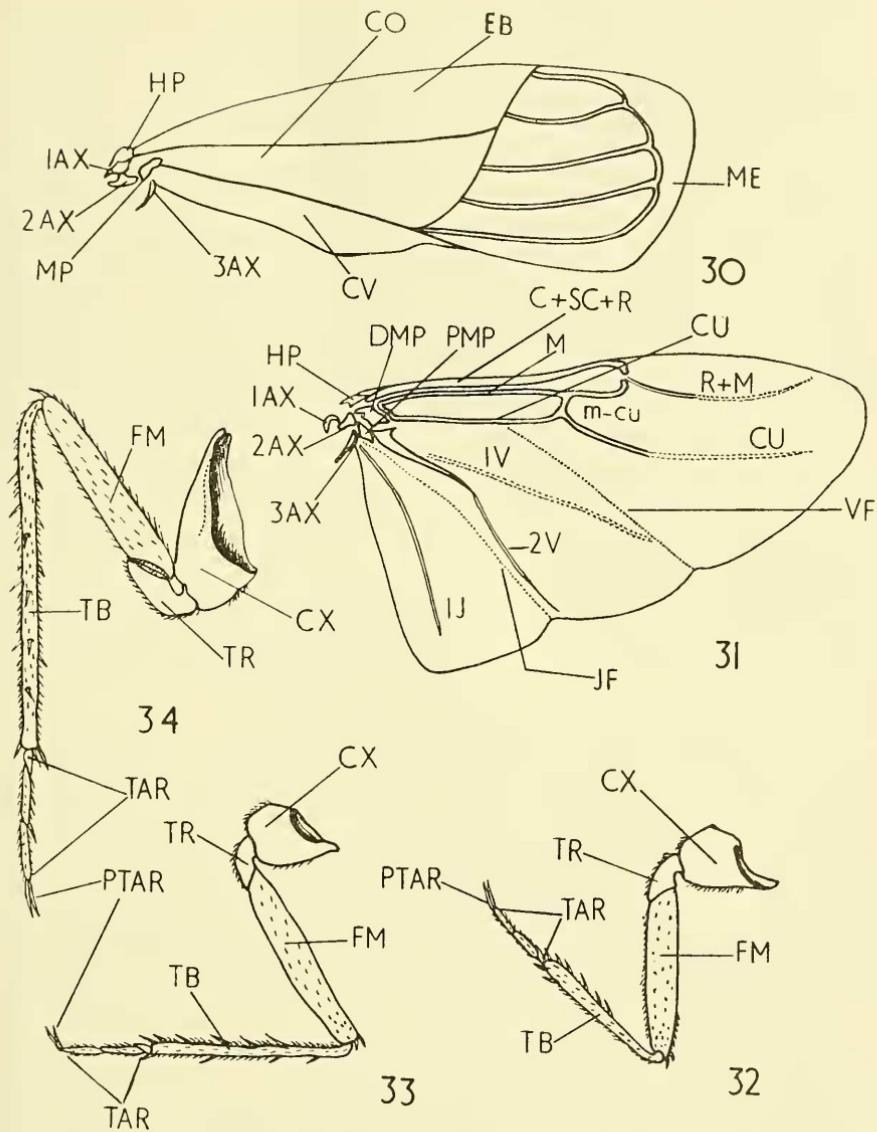
Abdomen very similar to that of *M. mulsanti*.

IV. MORPHOLOGICAL CONSIDERATIONS AND COMPARISONS

Head

Saldula palustris (Douglas). In the adult insect, on the anterodorsal part of the head capsule, the position of the frontal ecdysial cleavage line can be recognized by the position of the two pits; these are found on each side of the vertex along the frontal ecdysial cleavage line in the nymph. These two lateral pits are not homologous with the pretentoria of Cicadellidae (SPOONER, 1938). They have no counterparts in other Heteroptera as far as is known, and the name epicranial pits is here suggested for these structures. It should be mentioned that the frons is not always delimited laterally by the ecdysial cleavage line, for SNODGRASS (1960) states, "they vary greatly in their extent and position in different insects." He suggested the name cephalic apotome for the part cut out at ecdysis by the ecdysial cleavage line.

In *Saldula* the fronto-clypeal sulcus is absent, and consequently there is no external demarcation between the frons and the clypeus. The positions of the antafossae or the mandibular levers are often used as landmarks to delimit the frontal and clypeal areas (SPOONER, 1938). However, in *Saldula* they are situated cephalad and so are perhaps unreliable. These areas can be distinguished, however, by muscle attachment; the dilator muscles of the sucking pump are attached to the clypeus internally (SNODGRASS, 1935). SNODGRASS (1960) stated that the cibarium has often been called the 'pharynx' although it lies outside the mouth. He further stated that this cibarium has become the sucking pump of the liquid-feeding insects. It is evident, therefore, that the term pharyngeal pump is in-



Figs. 30—31. Wings of *Saldula*: (30) fore wing; (31) hind wing. Figs. 32—34. Legs of *Saldula*: (32) fore leg; (33) middle leg; (34) hind leg.

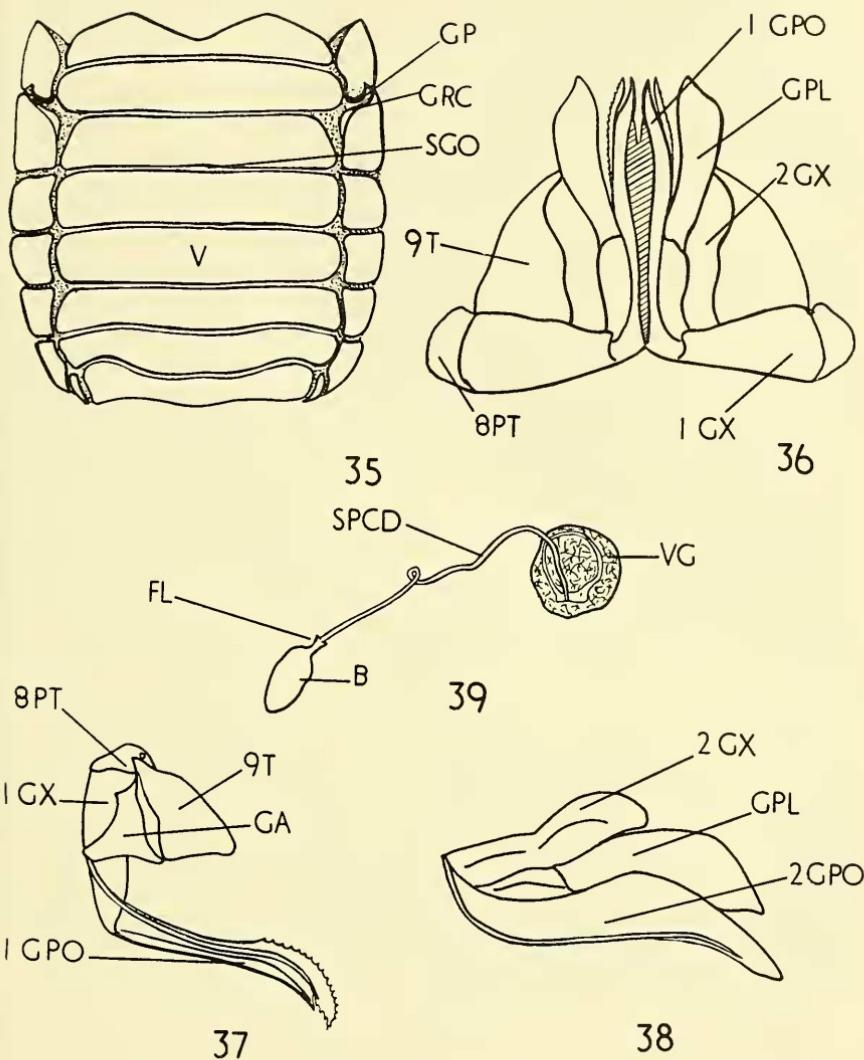
accurate. In *Saldula* the criterion of the muscle attachment has been used to delimit the frontal and the clypeal areas, although it is realized that this procedure is open to some criticism. For example, FERRIS (1944), DU PORTE (1946), and PARSONS (1959) have criticized the criterion of muscle attachment for the identification of the sclerites. The latter in her account of *Gelastocoris* used the frontal ganglion as landmark to delimit the point of attachment of the dilator muscle of the food-pump. She recognized two sets of muscles: cibarial, which lie

posterior to the frontal ganglion and attach on the clypeus, and pharyngeal muscles, which lie posterior to the frontal ganglion and attach on the frons. In this she followed MARKS (1959). PARSONS (1959), however, suggests, "that the muscle posterior to the frontal ganglion could come to insert on a cibarial portion of the food-pump, or that cibarial muscles might shift their insertions to the pharyngeal portion." She further quoted MARKS (1959) and stated that the position of the frontal ganglion also varies relative to the muscles from one species to another. It is evident then that an interpretation based on the position of the frontal ganglion is neither reliable. In the present study, therefore, in the absence of any alternative, the criterion of muscle attachment has been adopted to delimit the frontal and the clypeal portions of the head capsule. Examination shows that the dilator muscles of the sucking pump attach to a definite part of the head capsule, and so it is probably correct to interpret this area as the clypeus. EKBLOM (1926) states that in *Saldula saltatoria* (Lat.), "the forehead forms in front a transverse ridge where it limits the clypeus." This ridge would appear to be merely the posterior margins of the unpigmented postclypeal areas. In *Saldula*, therefore, as in other Heteroptera, the clypeus appears to be differentiated into a postclypeus, which is united with the frons, a distinct anteclypeal region, and two paraclypeal lobes.

The anteclypeus is a clearly defined area, and appears externally as a convex lobe, its internal concavity together with its lateral invaginations form a supporting base for the food-pump. To the cephalic margin of the anteclypeus is attached the flap-like labrum.

The paraclypeal lobes are well defined areas on each side of the anteclypeus; they extend caudad up to half the length of the latter. They are clearly visible in both the nymph and the adult, and appear to have no internal muscle attachment. The homology of the paraclypeal lobes in the Hemiptera is very controversial, and has been the subject of much debate. SMITH (1892) and WEBER (1929) considered them to be homologous with the mandibular plates. SNODGRASS (1935) also mentions, "that these paraclypeal lobes appear to be the mandibular plates of the Homoptera," but he himself doubted their mandibular origin in the Homoptera in the absence of any embryological evidence. EKBLOM (1926) and COBBEN (1960) designated these lobes in *Saldula saltatoria* as "laminae maxillares" and "maxillare Platten" respectively. PARSONS (1959) stated that the paraclypeus in *Gelastocoris* is wholly inflected within the head. However, most authors consider the paraclypeal lobes as parts of the clypeus. MUIR & KERSHAW (1911, 1912) regarded them as "extensions of the clypeus", and confirmed that "they have no relation to the mandibles." SFOONER (1938) stated that the paraclypeal lobes are undoubtedly parts of the clypeus. MACGILL (1947) referred to these two lobes in *Dysdercus intermedius* Distant as *juga*.

It is usually not possible to trace the mandibular plates in the Heteroptera since there is no sulcus between the mandibular plate area and the gena. It is, therefore, advisable to consider the whole area of the head capsule between the eye and the points of attachment of the mouthparts as the genal area; if mandibular plate area need to be recognized, it is suggested that it be defined as the ventro-anterior area of the gena to which the mandible articulates.



Figs. 35—39. Abdomen and female genitalia of *Saldula*: (35) dorsal view of abdomen of male; (36) ventral view of female terminalia; (37) first gonocoxa and associated parts; (38) second gonocoxa and associated parts; (39) spermatheca

In mandibulate insects the maxillae are usually attached to the ventral part of the postocciput (SNODGRASS, 1935). It does not appear to be necessary to recognize a maxillary plate area despite the fact that such an area is usually described in the hemipterous head. Maxillary plates are absent in the primitive orthopteran type of the head, and usually cannot be defined by sulci in the hemipterous head.

The origin of what is herein termed the postgenal bridge has been a problem in the past. Many authors claim that the ventral region of the head is formed by

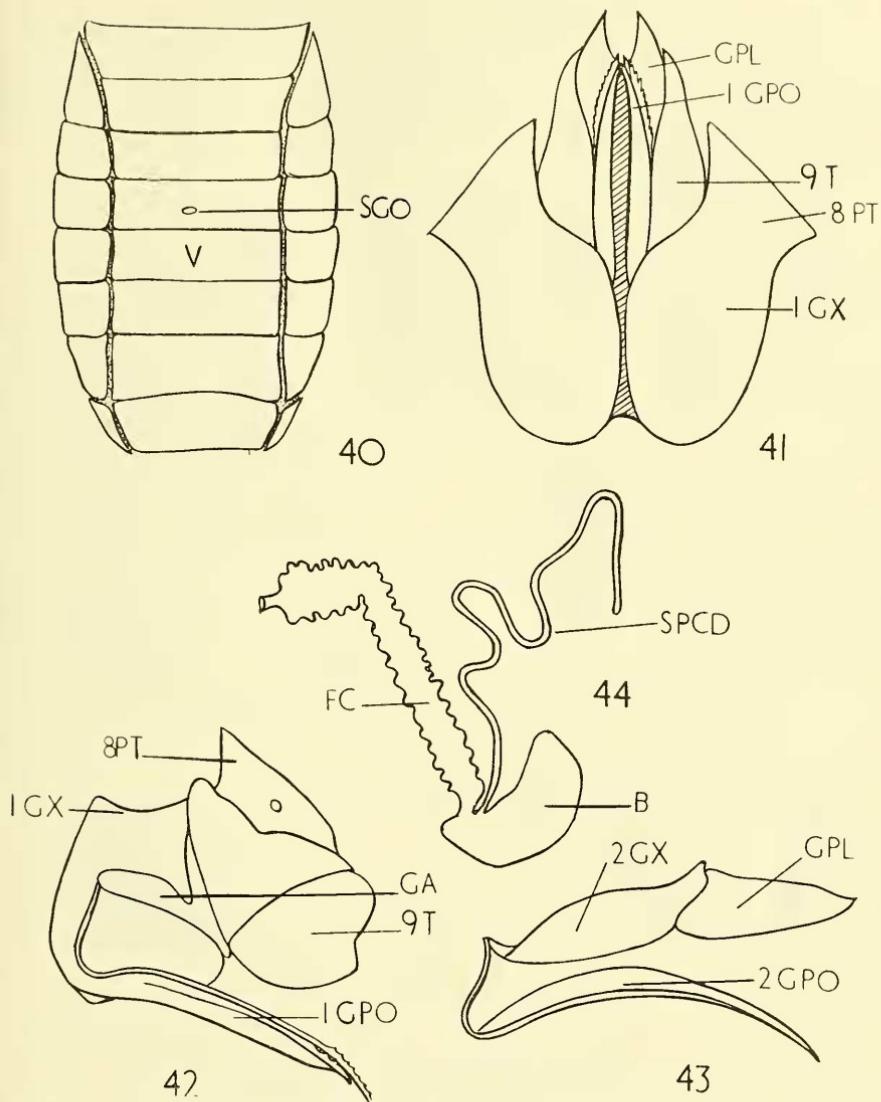
the fusion ventrally of the maxillary plates, the area considered to be equivalent to the postero-ventral part of the gena anterior to the point of articulation of the labium. MACGILL (1947) referred to the ventral area of the head in *Dysdercus intermedius* as a "large median ventral sclerite interpolated between the labium and the foramen magnum." However, she made no comment regarding its origin. PARSONS (1959), like most earlier authors, adopted the term "gula" but noted that perhaps it is not a true gula. SNODGRASS (1960) has recently considered the ventral sclerites of the head in insects, and has concluded that they are not homologous in all groups, and thus cannot in all be termed a "gula". He mentioned three distinct processes which may result in the formation of ventral sclerites of the head in insects: in the first, a hypostomal bridge may be formed between the occipital foramen and the base of the labium by the ventral fusion of two hypostomal lobes as in the Diptera. The hypostomal bridge, he stated, is continuous dorsally with the postocciput. The second modification, according to SNODGRASS, is the ventral fusion of two postgenal lobes forming a postgenal bridge between the occipital foramen and the base of the labium, as in *Vespa maculata*. When this is the case, the hypostomal bridge is replaced by the postgenal bridge, which differs from the former in not being continuous dorsally with postocciput. He thus regarded the ventral plate in *Notonecta* and *Naucoris* as the postgenal bridge since it is continuous with the postgenae and not with the postocciput. The third process described by SNODGRASS is the ventral fusion of the lower ends of the postocciput to form a median plate, which may become extended distally as in Coleoptera. This median plate is the true gula, and is continuous proximally with the postocciput.

In *Saldula* as in *Notonecta* and *Naucoris*, the ventral plate seems to be formed by the fusion ventrally of the postgenae. However, a developmental study of this region is badly needed to determine whether or not the homology accepted in the present study is really the correct one. This study should include a consideration of the origin of the bucculae. These structures, which apparently serve to support the rostrum during feeding, are interpreted as the ventral extensions of the areas anterior to the point of attachment of the labium. Since they often extend posterior to the rostrum, this interpretation is perhaps incorrect.

Thorax

The prothorax in *Saldula* is more or less of a generalized type seen in other Heteroptera in that it shows no differentiation into separate sclerites. The presence of the dome-shaped callal area does not seem to be a constant feature in the Saldidae, for DRAKE & CHAPMAN (1958) stated that a callus is absent in the genus *Saldoida*.

Of the three thoracic segments, the mesothorax in *Saldula* is the most developed. This agrees with WEBER's (1930) thesis that in the Hemiptera the fore wings are the principal organs of flight. Both the mesoscutellum and mesosternum are well developed. TAYLOR (1918) stated that in the Heteroptera the mesothoracic sternum is indistinguishably fused with the pleura. This is true in *Saldula*, and it is because of this fusion that the limits of the pleural and sternal sclerites cannot



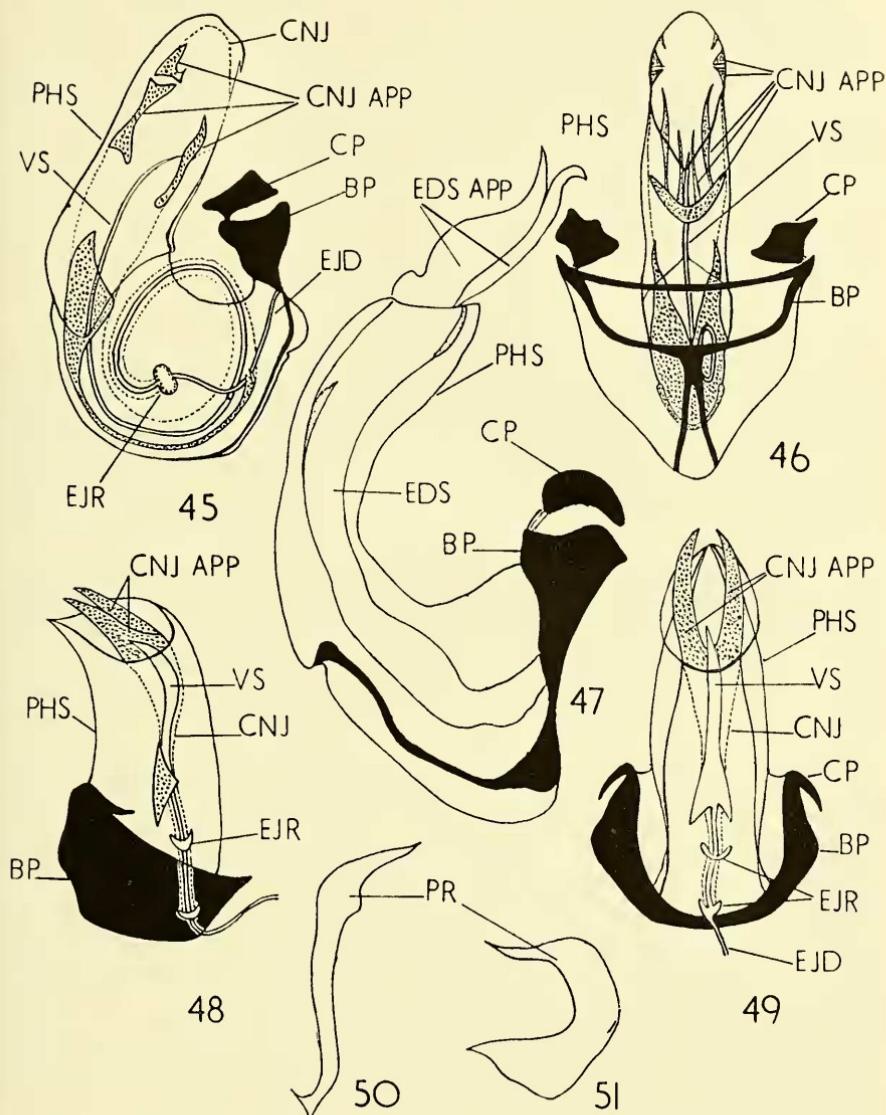
Figs. 40—44. Abdomen and female genitalia of *Mesovelia mulsanti*: (40) dorsal view of abdomen of female; (41) ventral view of female terminalia; (42) first gonocoxa and associated parts; (43) second gonocoxa and associated parts; (44) spermatheca

be clearly defined. The fusion of the sternopleural sclerotizations is also seen in the metathorax. BRINDLEY (1934) figured the thorax of *Saldula pilosella* (Thomson), and labeled the anterior and posterior areas of the mesosternum BS2 (basisternum of mesothorax) and BS3 (basisternum of metathorax), and left the middle area unnamed. If the location of the apophyseal pits is taken as the landmark in delimiting the sternal plates, her interpretation appears to be inaccurate with respect to the mesosternum. According to the interpretation given, the areas which she called BS2 and BS3 are merely the mesothoracic, presternum and

sternellum respectively. The basisternum of the metathorax in *Saldula* is a small plate, and lies beneath the mesosternellum, with the metasternal apophyseal pits lying on each side of it. This can be seen if the mesothorax and the metathorax are pulled apart. This structure is most clear in the nymph. Thus what BRINDLEY considered as the basisternum of the metathorax is evidently the sternellum of the mesothorax.

The pleural sulcus of the metathorax is horizontal, and lies on the margin of the pleura, so much so that the epimeron occupies a dorsal position, and is attached to the lateral margin of the metascutellum. According to TAYLOR (1918), the horizontal position of the pleural sulcus seems to be a general feature in the Heteroptera. BRINDLEY (1934) stated that this horizontal position is characteristic of the aquatic bugs because of the enlarged coxae, which extend behind rather than from beneath the thorax. LARSEN (1945) mentioned a horizontal pleural ridge in *Salda muelleri* (Gmelin). The upper forward margin of the metapleuron extends forwards beneath the posterior margin of the mesopleuron, and terminates in the metapleural wing process in the region of the mesepimeron. TAYLOR (1918) mentioned that similar condition is seen in the Nabidae, Gerridae and Berytidae. However, the metapleural wing process in *Saldula* is peculiar in that it is also supported by processes from the mesepimeron and the metascutellum, and lies in the region of the mesothorax. The large precoxal shelves of the metapleuron seem to be associated with the greatest development of the hind coxae.

In the fore wing, the corium is secondarily divided into a marginal embolium. DRAKE and CHAPMAN (1958) also mentioned an embolium in the genus *Saldoida*. In the interpretation of the veins of the hind wing of *Saldula* the criterion of the axillaries and their association with particular veins has been adopted. Thus the veins in association with the distal median plate have been designated as the media and cubitus, the former together with the radius seem to be very much approximated toward the costa and subcosta. It may be mentioned here that different degrees of fusion of the costa, subcosta, and radius occur also in the Miridae, Lygaeidae, Phymatidae, Mesoveliidae, and Piesmidae (HOKE, 1926). DRAKE and DAVIS (1958) have figured the hind wing of the piesmid *Miespa splendida* Drake, and have shown the cubitus in the same position as in *Saldula*. HOKE (1926) has studied the venation of the hind wings of the Heteroptera in detail. She followed the COMSTOCK-NEEDHAM system, and divided the wing into four areas: the costal area with costa, subcosta, radius and media 1 and 2; medial area with media 3 and 4; cubital area with cubitus and first anal, and the anal area with the remaining anal veins. On comparison, it becomes obvious that her cubital area in *Salda bouchervillei* Prov. (= *coriacea* Uhler) and *Saldula pallipes* (F.) (= *separata* Uhler) should really be interpreted as the vannal area, and thus it appears that the vein which she designated as cubitus is probably one of the vannal veins (Table I). Although she has omitted the consideration of the axillaries in her interpretation, she has figured them in the two saldids she studied, and it is evident that her cubitus is not in association with the distal median plate, which it should be according to the interpretation (SNODGRASS, 1935) adopted in the present study. Since many of the veins of the adult wing in the Heteroptera are without a corresponding trachea (HOKE, 1926) the inter-



Figs. 45—46 and 50. Male genitalia of *Saldula*: (45) lateral view of aedeagus and associated structures; (46) frontal view of aedeagus and associated structures; (50) paramere. Fig. 47. *Aepophilus bonnairei*: lateral view of aedeagus and associated parts. Figs. 48—49 and 51. Male genitalia of *Mesovelia mulsanti*: (48) lateral view of aedeagus and associated parts; (49) frontal view of aedeagus and associated parts; (51) paramere.

pretation of the adult veins seems to be more reliable if based on the associated axillaries. Very little information is obtained by studying the position of the trachea in the nymph. A reinterpretation of the wing venation of the Heteroptera based on the association of veins with axillaries is thus needed.

TABLE I. INTERPRETATION OF THE VEINS OF THE HIND WING

HOKKE	GUPTA
Costa	Costa
Subcosta	Subcosta
Radius	Media
r-m	m-cu
Media 1 plus 2	Cubitus
Cubitus	Vannal 1
Anal 1	Vannal 2
Anal 2	Jugal 1

Abdomen

DRAKE and HOTTES (1951) stated that "the hardened and plate-like and roughened lobe of the first paratergite together with the "peg-like" or "spine-like" organs of the second paratergite form the stridulatory organ in the Saldidae. LESTON (1957), however, stated that the granulated plate and the pegs were actually situated on the second and third paratergites respectively, and not on the first and second as indicated by DRAKE and HOTTES. LESTON also stated that the organ functions not as a stridulator but as clasping mechanism in the male during copulation. Examination of the organ in *Saldula* has revealed, however, that one small modification is needed in LESTON's description; the pegs are located actually on a fold of the conjunctiva underneath the anterior margin of the third paratergite and not on the anterior margin of the paratergite itself.

In the male genitalia, the sclerotized curved structure in the base of the conjunctiva probably acts as a guiding mechanism for the vesica, which passes along the ventral surface of this sclerite; the vesica is then directed on to the V-shaped structure in the ventral wall of the conjunctiva and is thus everted. PRUTHI (1925), in his account of the male genitalia of *Chilocanthus pilosus* (Fall.) and *Salda littoralis* (L.) did not mention the conjunctival appendages, the ejaculatory reservoir, and the capitate processes. The latter, according to MARKS (1951), are secondary developments in the Heteroptera, and mark the original points of attachment of the parameres to the basal plates. EKBLOM (1926) also failed to notice the ejaculatory reservoir and the capitate processes.

PRUTHI (1925) mentioned that the aedeagus in *Mesovelia* is not differentiated into phallosoma and endosoma, but examination of *Mesovelia mulsanti* has shown that the phallosoma, conjunctiva and vesica are distinguishable. EKBLOM (1928) figured a drawn-out endosoma with its two appendages in his account of *Mesovelia furcata*.

COMPARISONS

Head

On comparing the head structures of the two families, it is found that *Saldula* and *Mesovelia* resemble each other in a number of features namely, the well

developed vertex, the indistinct coronal and frontal ecdysial cleavage lines in the adult, the well developed clypeal regions, the absence of the frontoclypeal sulci, the four-jointed labium, the antennae, and in the possession of four pairs of cephalic trichobothria in the nymphs. However, these similarities lay not in characters of great taxonomic importance in the group. There are a number of important features in which they are quite distinct (Table II). It should be mentioned that although *Aepophilus bonnairei* appears to resemble *Mesovelia* more than *Saldula*, in respect of the most important taxonomic characters (that is, the shape of the mandibular lever, the presence of epicranial pits, and the absence of epipharyngeal process), *Aepophilus* is exactly like *Saldula*. It is evident that the two families, the Saldidae and Mesoveliidae, show more differences than resemblances in their head structures, and thus it is concluded that in the head structure they are distinct morphologically. The epicranial pits are a feature which appears to be confined to the Saldidae and can thus be regarded as a character by which this family can be separated from all other Heteroptera. However, other genera must be examined to ascertain that these structures are actually a constant feature in the family.

Thorax

In respect to the thoracic structures we also find that the Saldidae and the Mesoveliidae show certain resemblances, particularly in the pronotal collar, callal area with its median or lateral depressions, precoxal shelf, trochantin, and fused metascutum and scutellum, well developed coxae, flattened femora, and three tarsomeres, etc., but they exhibit distinct differences (Table II) which outweigh the resemblances. A preliminary examination of some of the families of the four higher taxonomic groups of the Heteroptera, namely Pentatomomorpha, Cimicomorpha, Amphibicorisae and Hydrocorisae, revealed that the structure of the mesonotum and the metasternum in the various families are of either *Saldula*-type (the mesosternum projecting over the metasternum) or *Mesovelia*-type (the mesosternum not projecting over the metasternum). Examination also revealed that, with the exception of the Amphibicorisae, the three groups possess both types (GUPTA, in press). This indicates that if the above mentioned taxa are natural groups, the structure of the thorax is of little value in distinguishing the suprafamilial categories.

Abdomen

On comparing the structure of the female genitalia, the aedeagus, the presence of ejaculatory reservoir, paratergites, and the seven pairs of abdominal spiracles, the two families are found to be very similar, but it is evident that other characters indicate that they are taxonomically distinct (Table II).

From the foregoing study it is evident that the Saldidae and the Mesoveliidae are not closely related as suggested by the comparative morphological study of the female genitalia; they are quite distinct in other morphological features.

COMPARISON OF ALATE AND APTEROUS (AND BRACHYPTEROUS) FORMS IN THE
SALDIDAE AND MESOVELIIDAE

From the comparative morphology of the alate and the apterous forms in both the Saldidae and the Mesoveliidae, it was found that these two groups show distinct structural differences, particularly in the thorax (Table III). Insects with flight possess well developed flight muscles and correlated with them an elaborate thoracic structure, while those with limited or no flight have reduced flight muscles, and consequently less developed thoracic structure. Flight in insects is effected by two sets of muscles, the direct and the indirect. The indirect muscles include the dorsal longitudinal muscles and the dorso-ventral muscles. The direct muscles are attached to wing bases or wing sclerites and include principally the basalar, the subalar and the muscles of the axillaries.

According to LARSEN (1945), the principal muscles are present in *Saldula*, and accordingly, as one would expect, the apodemes and the internal margin of the pronotal collar are well developed in the prothorax. The longitudinal muscles, running from the first phragma to the second phragma in the pterothorax, mainly produce the arching of the nota, and thus raising the notal processes relative to the pleural processes, act as depressors of the wing. And since these muscles are important in flight, the phragmata in *Saldula* are well developed. Similarly the development of the furca seems to be correlated with the development of the direct muscle, *m. furca-pleuralis* (of LARSEN). By the same token, the absence of another direct muscle, *m. coxa-subalaris* (of LARSEN) both in the mesothorax and the metathorax is correlated with the absence of the subalar sclerites in the pterothorax. The lateral oblique muscle, *m. mesonotis secundus* (of LARSEN) is well developed in the mesothorax of *Saldula*, but is absent in the metathorax. This can be explained on the basis of WEBER's thesis that in the Heteroptera the fore wings are principal organs of flight, and thus the mesothorax is more developed than the metathorax. It is evident from the foregoing that the morphological differences are the reflections of the functional differences in the alate and the apterous forms. Unfortunately, no account of the musculature of *Mesovelia* is available for comparison, but the structural differences in the thorax of *Mesovelia vittigera* and *M. mulsanti* could also be explained on a functional basis. This study has also revealed that the sternal region in the alate and the apterous forms shows very little difference, and thus perhaps the dorso-ventral muscles are not of great importance in the flight of these insects.

On comparing the alate and the apterous forms of both families, it is found that the ocelli are rudimentary or absent in the apterous forms, but are present in the alate forms. Accompanied with this presence of the ocelli in the alate forms, are well developed compound eyes, which are not so conspicuous in the apterous forms. Such correlated presence or absence of certain structures has also been reported in the Lygaeidae (SCUDDER, personal communication). It is likely that perhaps an alate insect needs more perfect visual apparatus than an apterous one, and probably the ocelli supplement the compound eyes in their visual perception. It is also possible that the presence of the ocelli in the alate forms and its absence in the apterous may be due in part to a genetic linkage with some other

character affected by the loss of flight.

The systematic position of the Saldidae and the Mesovelidiidae, based on their morphology, has been considered elsewhere (GUPTA, in press).

TABLE II. DIFFERENCES IN THE STRUCTURES OF HEAD, THORAX AND ABDOMEN

Parts	Saldidae	Mesovelidiidae
HEAD		
(1) Postclypeus.	(1) Cephalic portion of postclypeus with two lateral unpigmented areas (absent in nymph); absent in <i>Aepophilus</i> .	(1) No such unpigmented areas present.
(2) Paraclypeal region	(2) Well defined in <i>Saldula</i> ; not so in <i>Aepophilus</i> .	(2) Not well defined.
(3) Bucculae.	(3) Well developed in <i>Saldula</i> ; not so in <i>Aepophilus</i> .	(3) Not well developed.
(4) Postgenal bridge.	(4) Short in <i>Saldula</i> ; longer in <i>Aepophilus</i> .	(4) Longer than in <i>Saldula</i> .
(5) Mandibular lever.	(5) Triangular both in <i>Saldula</i> and <i>Aepophilus</i> .	(5) Roughly quadrangular.
(6) Postocciput.	(6) Differentiated into dorsal and lateral portions in <i>Saldula</i> ; not so in <i>Aepophilus</i> .	(6) Not so differentiated.
(7) Maxillary plate area.	(7) Not developed dorsally in <i>Saldula</i> ; developed dorsally in <i>Aepophilus</i> .	(7) Developed dorsally.
(8) Labrum.	(8) Without epipharyngeal process both in <i>Saldula</i> and <i>Aepophilus</i> .	(8) With epipharyngeal process.
(9) Cephalic trichobothria.	(9) Eight to ten pairs in adult <i>Saldula</i> ; four pairs in <i>Aepophilus</i> .	(9) Three pairs in the adult.
(10) Compound eyes.	(10) Conspicuous in <i>Saldula</i> not so in <i>Aepophilus</i> .	(10) Not so conspicuous as in <i>Saldula</i> .
(11) Ocelli.	(11) Present in <i>Saldula</i> ; absent in <i>Aepophilus</i> .	(11) Rudimentary in <i>Mesovelia mulsanti</i> ; present in <i>M. vittigera</i> .
(12) Epicranial pits.	(12) Present both in <i>Saldula</i> and <i>Aepophilus</i> .	(12) Absent.
THORAX		
(13) Scutellum (mesoth.).	(13) Extends over second abdominal segment in <i>Saldula</i> ; not so in <i>Aepophilus</i> .	(13) Does not extend over abdomen.
(14) Parascutellum (mesothorax).	(14) Present in <i>Saldula</i> ; absent in <i>Aepophilus</i> .	(14) Absent.
(15) Pleural sulcus (mesothorax).	(15) Distinct but short in both.	(15) Indistinguishable in both.

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| (16) Epimeron (mesoth.). | (16) Divided into dorsal anepimeron and ventral katepimeron. | (16) Not so divided in both. |
| (17) Sternum (mesoth.). | (17) Sternellum extending over metasternum in both. | (17) Sternellum not extending over metasternum. |
| (18) Coxal cleft (metathorax). | (18) Present in both. | (18) Absent in both. |
| (19) Pleural sulcus (metathorax). | (19) Present and dorsal in both. | (19) Absent in both. |
| (20) Orifice of scent apparatus. | (20) Two, located laterally. | (20) One, median in position. |
| (21) Fore wings. | (21) Differentiated into clavus, embolium and membranous part. | (21) Mostly membranous. |
| (22) Hind wings. | (22) With jugal fold. | (22) Without jugal fold. |
| (23) Base of media. | (23) Not fused to costa, subcosta and radius. | (23) Fused to costa, subcosta and radius. |
| (24) Tibial comb. | (24) Absent in both. | (24) Fore and middle tibiae with combs at distal ends. |
| (25) Pseudo-aratiae (parempodium). | (25) Absent. | (25) Present. |

ABDOMEN

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| (26) Apodeme in sternum VII. | (26) Absent. | (26) Present. |
| (27) Clasping organ. | (27) Present. | (27) Absent. |
| (28) Aedeagus. | (28) Differentiated into phallosoma, conjunctiva and vesica in <i>Saldula</i> ; in <i>Aepophilus</i> , into phallosoma and endosoma only. | (28) Differentiated into phallosoma, conjunctiva and vesica. |
| (29) Base of phallosoma. | (29) Supported by an inverted Y-shaped structure in <i>Saldula</i> ; by L-shaped structure in <i>Aepophilus</i> . | (29) Absent. |
| (30) Conjunctiva. | (30) Dorsal half sclerotized into a curved structure in both. | (30) Present. |
| (31) Ejaculatory reservoir. | (31) One. | (31) Two. |
| (32) Parameres. | (32) Sickle-shaped. | (32) Hook-like. |

TABLE III. DIFFERENCES IN THE ALATE AND APTEROUS (BRACHYPTEROUS) FORMS
IN THE SALDIDAE AND THE MESOVELIIDAE

Parts	Alate form	Aptero (brachypterous) form
(1) Callal area.	(1) Present.	<i>Saldula palustris</i> (1) Absent.
(2) Furcal arms.	(2) Well developed.	<i>Aepophilus bonnairei</i> (2) Not well developed.
(3) Mesoscutellum.	(3) Extends over the abdomen.	(3) Does not extend over the abdomen.
(4) Ocelli.	(4) Present.	(4) Absent.
(1) Callal area.	<i>Mesovelia vittigera</i> . (1) Present.	<i>Mesovelia mulsanti</i> . (1) Rudimentary.
(2) Mesonotum.	(2) Differentiated into mesoscutum and scutellum, the former being overlapped by the posterior part of the pronotum.	(2) Mesonotum undifferentiated.
(3) Metanotum.	(3) Median part extending over abdomen.	(3) Does not extend over abdomen.
(4) Ocelli.	(4) Present.	(4) Rudimentary.

KEY TO LETTERING OF FIGURES

A	— anal vein	EDS APP	— endosomal appendages
AC	— anteclypeus	EJD	— ejaculatory duct
AEM	— anepimeron	EJR	— ejaculatory reservoir
AF	— antafossae	1 EM	— epimeron of prothorax
ANP	— anterior notal wing process	2 EM	— „ „ mesothorax
AP	— apodemes	3 EM	— „ „ metathorax
APP	— apophyseal pits	EPP	— epipharyngeal process
AS	— antennal tubercle	1 ES	— episternum of prothorax
AT	— antenna	2 ES	— „ „ mesothorax
1 AX	— first axillary	3 ES	— „ „ metathorax
2 AX	— second axillary	FC	— fecundation canal
3 AX	— third axillary	FL	— flange of pump
B	— spermathecal bulb	FM	— femur
BP	— basal plates	FR	— frons
1 BS	— basisternum of prothorax	FU	— furca
2 BS	— „ „ mesothorax	FWP	— fore wing process
3 BS	— „ „ metathorax	G	— gena
BU	— bucculae	GA	— gonangulum
C	— costa	GP	— granular plate of clasping organ
CA	— callus	GPC	— concavity of clasping organ
CE	— compound eye	GPL	— gonoplac
CL	— clypeus	1 GPO	— first gonapophysis
CNJ	— conjunctiva	2 GPO	— second gonapophysis
CNJ APP	— conjunctival appendages	1 GX	— first gonocoxa
CO	— corium	2 GX	— second gonocoxa
CP	— capitate processes	HP	— humeral plate
CT	— coxal cleft	HWP	— hind wing process
CU	— cubitus	J	— jugal vein
CV	— clavus	JF	— jugal fold
CX	— coxa	KEM	— katepimeron
DMP	— distal median process	L	— labium
EP	— epicranial pit	LB	— labrum
EDS	— endosoma		

M	— media	PS	— pleural sulcus
ME	— membrane	PSCU	— parascutellum
MP	— median plate	2 PSL	— postscutellum of mesothorax
MSN	— mesonotum	3 PSL	— " " metathorax
MTN	— metanotum	PSN	— postnotum
MXPA	— maxillary plate area	PT	— paratergite
N	— notum	PTAR	— pretarsus
O	— ocellus	R	— radius
OC	— occiput	SC	— subcosta
OCC	— occipital condyle	2 SCL	— mesoscutellum
OF	— occipital foramen	3 SCL	— metascutellum
PAC	— paraclypeus	2 SCU	— mesoscutum
PC	— postclypeus	3 SCU	— metascutum
PCS	— precoxal shelf	SGO	— scent gland orifice
PG	— postgena	SPCD	— spermathecal duct
PGB	— postgenal bridge	ST	— stigma
2 PH	— phragma of mesothorax	1 STL	— sternellum of prothorax
3 PH	— " " metathorax	2 STL	— " " mesothorax
PHS	— phallosoma	T	— tergum
PHS APP	— phallosomal appendages	TAR	— tarsus
PLA	— pleurodema	TB	— tibia
PMP	— proximal median plate.	TN	— trochantin
PN	— pronotum	TR	— trochanter
PNC	— pronotal collar	1 V	— first vannal vein
PNP	— posterior notal wing process	2 V	— second vannal vein
PO	— postocciput	VF	— vannal fold
PR	— paramere	VG	— vagina
1 PRS	— presternum of prothorax	VS	— vesica
2 PRS	— " " metathorax	VX	— vertex
PRSC	— prescutum	WP	— pleural wing process

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VI. SUMMARY

The systematic position of the Saldidae is controversial. SCUDDER (1959) suggested a close relationship between the Saldidae and the Mesoveliidae, based on his studies of their female genitalia. The morphology of these two families has been studied to throw some light on their probable relationship. It was found that these two families are distinct morphologically. Their systematic position has been considered elsewhere (GUPTA, in press).

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